

**VARIATION AMONG ACCOUNTS OF
DIEUNOMIA TRIANGULIFERA (VACHAL)
(HYMENOPTERA: HALICTIDAE)
IN DIFFERENT LOCALITIES AND YEARS**

CLARE T. WUELLNER

Department of Entomology, Snow Entomological Museum, Snow Hall,
University of Kansas, Lawrence, Kansas 66045¹

Abstract.—This paper presents data concerning the natural history of a gregarious halictid bee, *Dieunomia triangulifera* (Vachal) gathered over three field seasons (fall of 1994, 1995, and 1996). My findings were compared to similar published data. This comparison shows variation in many aspects of the natural history of this bee. Because most studies of natural history are based on a single field season's data, much variation is missed for lack of long-term, multiple site study.

Key Words.—Insecta, Hymenoptera, Halictidae, *Dieunomia triangulifera*, long-term study, solitary bee, natural history.

Countless papers about insects have been published based on data gathered from a single field season, or even a few days' study. Such papers are often used for reference and comparative studies. Comparisons made about natural history, behavior, behavioral ecology, etc. of a species based on such studies can be of limited value in determining plasticity and variability under changing environmental conditions, particularly in regions such as centers of large continents where annual weather variation can be erratic and great.

Except for the highly social species, studies of bees including more than one field season's data or fragments of several seasons are few. Yanega (1990) studied an aggregation of the primitively eusocial halictid bee, *Halictus rubicundus* (Christ)(Hymenoptera: Halictidae), for seven years. Not only did he observe important details of natural history, but he also was able to relate how the population structure resulting from the bees' philopatric behavior might be "conducive to the evolution and maintenance of social behavior." A long-term study of an aggregation of *Centris pallida* Fox (Hymenoptera: Apidae) used data from the years of 1974, 1982, and 1988 (Alcock 1989). After a single field season, Alcock (1989) determined that larger males were likely to out-compete smaller males in fights to determine which bee mated. Despite the apparent advantage of large size and presumed directional selection in this system, the ratio of large to small males did not change over the 14-year period. Alcock (1989) proposed that variation in larval provisioning by females is likely to be the mechanism by which size variation in males is maintained.

The importance of long-term studies is apparent when comparing reports from field seasons of different years. They often reveal variation in natural history of the organism that would not be apparent in only a single year. Even more variation can be found when studies are done at different sites. I have studied *Dieunomia*

¹ Present address: Fire Ant Laboratory, Brackenridge Field Laboratories, Department of Zoology, University of Texas, Austin, Texas 78712. email: ctw@mail.utexas.edu

triangulifera (Vachal) at one site (described below) for three field seasons. These data along with data from Minckley et al. (1994), also from the same site, and other publications based on research completed at other sites, offer an opportunity to explore variability in natural history of *D. triangulifera* among years and sites. This variability either directly or indirectly reflects how this bee interacts with biotic and abiotic factors. Examination of such variation as published here increases our understanding of how the environment, floral hosts, and natural enemies influence the biology of *D. triangulifera* and other solitary bee species.

GENERAL NATURAL HISTORY OF *DIEUNOMIA TRIANGULIFERA*

Dieunomia triangulifera begins to emerge in mid-August at my study site near Eudora (Douglas County), Kansas (38°57'30" N, 95°7'30" W), U.S.A. Males emerge before females and patrol the nesting aggregation for receptive females. Females mate shortly after emergence and then excavate their nests in the ground. The nest consists of a single vertical tunnel that is 30 to 110 cm deep, from which one or two side tunnels, called laterals, branch (Cross & Bohart 1960). Along the bottom of these laterals, the females excavate and provision cells, one at a time. The provisions are largely pollen collected from *Helianthus annuus* L. (Asteraceae). The pollen is compacted into a lens-shaped pollen ball, approximately 8.2 by 4.5 mm (Cross & Bohart 1960). Females are active and provision cells until mid- to late-September, depending on when the weather cools. Immatures overwinter as prepupae. By excavating nests and examining immatures, I have found that the bees begin to pupate approximately two weeks prior to emergence in mid-August.

VARIATION IN EMERGENCE PHENOLOGY

Cross (1958) examined museum specimens of *D. triangulifera* from throughout its range and found that most were collected between 10 Aug and 15 Sep, the earliest collection was a male on 7 Jul, and the latest was of a female on 2 Oct. The earliest I have seen males active was 15 Aug 1995, and the latest female activity was 2 Oct 1995 at the Eudora site.

Cross & Bohart (1960), studied *D. triangulifera* at sites in Utah and eastern Kansas and reported that males emerge "at least a week" before females. Data combined from Minckley et al. (1994, data from years 1987–1990) and my two field seasons (1995 and 1996) gave an average difference between male and female emergence dates of 2.8 d (SD = 2.137, min = 0, max = 5 d, $n = 6$). Given that adult bees are active an average of 34.3 d each year (SD = 4.5; 1995 = 39 d, 1996 = 34 d, 1998 = 30 d) and that female adult lifespan (based on nesting activity) was estimated to be 13.2 d (Minckley et al. 1994), protandry of at least a week's time (> 50% of the adult lifespan) versus approximately 3 d (~20% of the adult lifespan) seems considerably different.

Long-term studies can reveal correlations that have important ecological implications. At the Eudora site, the date of onset of female emergence varied from 12 to 21 Aug and the onset of nesting varied from 16 to 24 Aug. The onset of blooming of this specialist bee's pollen source varied from 12 to 24 Aug. Emergence of the bee coincides roughly with the onset of sunflower bloom (Minckley et al. 1994, Wuellner 1999).

Because *D. triangulifera* is an oligolectic bee specializing on pollen of *H.*

annuus, there is strong selection for emergence to be correlated with *H. annuus* flowering. The relatively small variation in onset of emergence probably reflects selection for synchronization of bee emergence and *H. annuus* bloom. All studies that mention onset of *D. triangulifera* emergence contain statements regarding this relationship (Cross & Bohart 1960, Minckley et al. 1994, and Wuellner 1999).

The three-year study by Minckley et al. (1994) found evidence that availability of the host plant influenced the reproductive success of the aggregation: the year following abundant pollen resources, the aggregation increased in size. Conversely, in the year following relatively low pollen resources, the number of bees in the aggregation decreased.

The mass emergence of *D. triangulifera* females which provision their nests only with *H. annuus* pollen should have consequences for other bees that use *H. annuus*. Cross & Bohart (1960) and Minckley et al. (1994) found that although many species of bees use *H. annuus* pollen, the number of species at flowers drops at sites with *D. triangulifera* at about the time when it is provisioning nests. Clearly, the synchronization of female emergence and activity with bloom phenology of *H. annuus* increases competition with other species for this resource of pollen and nectar.

VARIATION IN FEMALE DAILY ACTIVITY

To published reports on female daily activity, I add observations about how weather conditions influence activity, and observations of orientation behavior and how it changes during the day.

Females of *D. triangulifera* are active during daylight hours when no precipitation is falling and when the ambient temperature is above approximately 18° C. The average temperature at which activity began was 18.19 °C (SD = 1.56, min = 16.3 °C, max = 21.4 °C, $n = 10$). Minckley et al. (1994) also reported activity in the Eudora aggregation at a minimum of 18 °C. Each day, a foraging female exits her nest, takes flight, and makes an orientation flight. The orientation flight is similar to that of other bees (described in Jander (1997) as “focal exploration” and “peripheral exploration”) to memorize the location of her nest. She then leaves the aggregation to forage.

Females are most often found foraging for nectar on *H. annuus*, although they take nectar from a variety of flowers (Hurd et al. 1980). However, they use mostly pollen from *H. annuus* to provision their nests (Minckley et al. 1994). Once the female has completed her foraging trip, she returns to her nest. Females spend as little as 7 to 8 min in the nest before leaving again. During that time the female grooms off the pollen load, and completes other activities such as making the pollen ball, excavating parts of the nest and/or of a cell, grooming, and resting. Females often make more than one foraging trip in a day (details below). After returning from their first foraging trips of the day, departing females have their nest locations memorized and make no orientation flights; they simply fly straight from the nest entrance.

Start of daily activity was reported by Minckley et al. (1994) to be 07:30 h when ambient temperature had reached 18 °C, but this result was based on only one detailed observation. I have found that the time of day that activity begins is related to ambient temperature. At the beginning of the field season, when temperatures are relatively warm, activity begins around 07:00 h. By the end of the

field season, the time of day at which the temperature reaches 18 °C is later in the morning, and activity begins around 11:00 h. To test the hypothesis that ambient temperature is what cues daily emergence, in 1994 on three mornings before any bees in the aggregation had emerged for the day, I provided artificial heat with an infrared heating lamp (so that the bees could see no light). Bees under artificial heating emerged at an average temperature of 47.4 °C (SD = 6.93, min = 38.0 °C, max = 56.5 °C, $n = 10$) at an average of 56 min (SD = 6.95, min = 50 minutes, max = 63 minutes, $n = 7$) before unheated bees in the aggregation. These “early risers” began their orientation flights, but, as soon as they flew away from the heat source, they fell to the ground and sat until ambient temperature increased to enough for normal activity (~18 °C). That such extreme temperatures were required to elicit early emergence suggests that temperature is not the only factor influencing time of emergence.

The briefest foraging trips are the first trips of the day, when freshly dehiscid anthers provide abundant pollen (Minckley et al. 1994, Wuellner personal observation). Trip duration increases each hour until noon, reflecting reduction in pollen availability with harvesting. Minckley et al. (1994) also recorded activity through the afternoon and found that foraging trips increased in length into the mid-afternoon, but then decreased again toward sunset, when more pollen is released by the flowers.

Minckley et al. (1994) found that foraging trips per individual varied from 0–8 per day (Mean = $3.44 \pm$ SD 0.3, $n = 44$). From the field season of 1994, I also found that foraging trips per individual varied from 0–8 per day, but the mean number of trips was smaller (Mean = $2.86 \pm$ SD 0.3, $n = 82$).

Although female bees normally only enter their own nests, there are two instances in which they enter other bees' nests (Minckley et al. 1994, Wuellner 1999). Minckley et al. (1994) and Cross & Bohart (1960) both have mentioned behavior typical of what I have called “lost” bees (Wuellner 1999). “Lost” bees are bees that search intensely in an area that is usually no larger than 10×10 cm. They often repeat the reverse orientation flight, land, and then scuffle about in the dirt. They sometimes enter nests near their own, but then quickly exit. These bees invariably stop searching after entering their own nest. Nearly all “lost” bees have external pollen loads. In every case, once the pollen-covered “lost” bee enters her own nest, she emerges without the external pollen, indicating that she has provisioned a cell.

There is another instance in which bees enter nests other than their own. Some bees, “searching bees” (Wuellner 1999), clearly investigate areas larger than those investigated by “lost” bees. Searching bees never have external pollen and enter many nests in widely-separated areas of the aggregation. They are investigating the nests of conspecifics, either to locate vacant nests to claim as their own, or to cleptoparasitize their conspecifics (Wuellner 1999).

VARIATION IN NESTING BIOLOGY

Dieunomia triangulifera nests in aggregations, which can have from a few hundred to tens of thousands of bees. The nest density varies from 40/m² (Minckley et al. 1994), to 98/m² (Wuellner, unpublished data 1996), and as high as 311/m² (Rau 1929).

Dieunomia triangulifera prefers to nest on bare or sparsely vegetated soil

(Pierce 1904, Rau 1929, Cross & Bohart 1960). Rau (1929) and Pierce (1904) both report that *D. triangulifera* nests on ground that is slightly higher than surrounding ground (thus, the common name "knoll" bee). Cross & Bohart (1960) state that the "bees usually occupy knolls or gentle slopes, but in sandy washes or hard-packed clays they may choose level ground." At the Eudora site, females frequently nest in the dirt road. The road is, for the most part, the lowest ground at the site, but it is hard-packed.

Rau (1929) reports nesting in a soil type quite different from those reported in other publications. He reports an aggregation nesting on bare, yellow, "gummy" clay. This contrasts sharply with the clay loam, sandy loam, silt loam, and sandy soils reported by Cross & Bohart (1960), Cane (1992), and my own findings. Pierce (1904) states that the bees he studied nested on hard bare ground. I have seen these bees nest in soils of various hardness, including the hard soil of a dirt road. All of these cases contrast sharply with the yellow and "gummy" soil described by Rau (1929). The aggregations studied by Rau (1929) and Pierce (1904) both were active about a week earlier than those studied by Cross & Bohart (1960), Minckley et al. (1994), and me. Voucher specimens for Pierce (1904) from the University of Nebraska State Museum Systematics Research Collections (Lincoln, Nebraska) were confirmed to be *D. triangulifera*. However, the earlier emergence coupled with the difference in soil characteristics, raises some question as to whether Rau (1929) was studying *D. triangulifera* or some other species. No voucher specimens from Rau (1929) have been located.

VARIATION IN COMPOSITION OF NATURAL ENEMIES

An aggregation of nests is an obvious resource for natural enemies. I have found that causes of mortality for adult bees include predation by asilid flies and cicindellid beetles, and parasitism by conopid flies. Larvae in excavated cells ($n = \sim 300$) were killed by fungus, rhipiphorid larvae, meloid larvae, ants, and miltogrammine flies (Wuellner, unpublished data). Additionally, I have seen several species of mutillids investigating nests at the aggregation and several species of bombyliids flicking eggs into nest entrances. Forty-three cells on 31 Jul 1995 (15 days before onset of adult emergence) had 21 empty cells, 15 cells with prepupae, 5 cells with pupae, and 2 cells containing prepupae of *D. triangulifera* and rhipiphorid larvae. Only 47% of the cells contained living immatures of *D. triangulifera*.

Emergence traps are used to capture insects emerging from the soil at sites known to contain bee nests. Emergence traps were pyramid-shaped, screened-in cages with open bottoms. Three of the traps had bottom dimensions of 0.9×9.3 m, and 17 were 0.75×0.75 m. The traps rested on the ground with soil piled up over the bottom edges. Insects were funneled into a collecting container at the top. Emergence traps can be used to determine immature mortality rates by assuming that each emergent natural enemy represents one host bee destroyed. Numbers of emergent host bees and natural enemies are added together to give the total number of *D. triangulifera* that would have emerged had there been no natural enemies. Immature mortality due to natural enemies is then calculated as a percentage of the total number. This method misses natural enemies such as fungi, flightless natural enemies such as ants and female mutillids, and natural

enemies that emerged before the traps were installed, and therefore often underestimate mortality of bee larvae.

For *D. triangulifera*, Wcislo et al. (1994) used emergence traps to study mortality caused by six species of natural enemies. They found that mortality was approximately 10, 20, and 30% in 1988, 1989, and 1990, respectively. Using this same method, I found that mortality due to natural enemies was approximately 6% in 1995, and increased to approximately 11% in 1996. Therefore, annual mortality rate of immatures was as little as 6% and as great as 30%. A single year's study would have missed these fluctuations.

Not only does the overall mortality rate fluctuate from year to year, but the most prevalent natural enemy varies from location to location, and within one location, from year to year. Presence of natural enemies at nesting aggregations of *D. triangulifera* are reported in three papers. Pierce (1904) reported that predaceous *Cicindela* sp. (Coleoptera: Cicindellidae) were present at the aggregation he studied at Lincoln, Nebraska. Wcislo et al. (1994) reported five species of natural enemies in 1989 at the aggregation near Eudora, Kansas. The species were *Heterostylum croceum* Painter (Diptera: Bombyliidae), *Rhipiphorus solidaginus* Pierce (Coleoptera: Rhipiphoridae), *Triepeolus distinctus* Cresson (Hymenoptera: Apidae), *Zodion fulvifrons* Say (Diptera: Conopidae), and a mutillid wasp. The bee fly *H. croceum* was most prevalent in 1989 and 1990, and *R. solidaginus* was most prevalent in 1991. At the same aggregation in 1996, I found that the most numerous natural enemy was the rhipiphorid beetle, *R. solidaginus*.

DISCUSSION

From comparing data gathered by myself and others, it is clear that there is important variation in natural history that would have been missed if this species had been studied for a single field season. This is especially interesting with regard to the tri-trophic level interaction of host plant-bee-natural enemy. Natural enemy emergence is synchronized with emergence of their host, *D. triangulifera*. In turn, emergence of the bee closely mirrors onset of the host plant bloom. Although there is fairly close synchrony in timing of the phenologies of these three trophic levels, there is variation in their onset among years.

What cues and synchronizes these events? There is evidence for a physiological clock as well as temperature cues (Cross & Bohart 1960). Year round temperature regimes influence soil temperatures, which in turn probably influence synchrony of emergence of *D. triangulifera* with conspecifics; synchrony of *D. triangulifera* with their host plant; and synchrony of emergence of natural enemies with emergence of *D. triangulifera*. Understanding what cues each of these events will explain the close relationship seen among annual emergence patterns.

Variation seen in natural enemy load and composition of natural enemy species in this system warrants further study. Detailed studies of the natural history and foraging behavior of each species of natural enemy will provide the groundwork needed to determine how each of the natural enemies influences (and is influenced by) its host species.

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